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PATTERN DEVELOPMENT IN MAMMALS AND BIRDS

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THE particular coloring of mammals and birds is produced by two factors—pigmentation and the physical structure of the hair or feathers. Both are often present together. In certain mammals, for example the golden mole (*Chrysochloris*) and the European Galemys, a beautifully iridescent sheen is produced by the reflection of light rays having a certain angle of incidence upon the hairs which themselves contain pigment of a characteristic color. In the duckbill (*Ornithorhynchus*) the same thing is found. The peculiarity of feather structure that causes iridescence is largely developed in certain families of birds, as the hummingbirds and the pigeons (see Strong, 1904, for an account of the feather structure).

It is not my purpose to discuss the *use* of this iridescence to the bird, beyond stating my belief that it is in part at least for sexual display, as no one can doubt who watches the male street pigeon strutting before his mate. With amorous coos and lowered head, he confronts her and, swelling out his throat feathers, turns about and about, so that the light is reflected from his neck and throat in a sparkle of rainbow hues. It has also been suggested (Thayer, 1909) that iridescence may be a strong factor in concealment, since from the variety of the colors produced the bird is more difficult to resolve from its many tinted environment amid foliage and flowers.

With many birds the characteristic coloration may not be at all that of its pigment. Thus the blue of the male indigo bird (*Passerina cyanea*) is due solely to the physical structure of its feathers which though pigmented with brown, appear blue by reflected light. If, however, a blue feather be immersed in oil and viewed under a microscope by *transmitted* light, it is seen to be *brown*-pigmented. The physical feather-structure of the adult male is thus in this species a secondary sexual character chiefly developed during the breeding period.

The important point at present is, however, that the color effects just described are none the less due to pigment, quite apart from the fact that the apparent color of the pigmented area may be different from the actual color of the pigment (except that iridescence may sometimes be faintly seen in an unpigmented feather).

The use of pigmentation to its possessor is a matter still under discussion and investigation. In many cases it is doubtless the result of purely physical causes and it is quite without the power of the animal to make use of its coloration for outward effect. Thus the beautiful colors inside the shells of some molluscs are never apparent from an exterior view, and are supposed by some to be in part a waste product, the result of metabolism within the organism.

The present discussion has to do only with the external pigmentation of the hair and feathers, respectively, in mammals and birds.

The simplest cases of coloration are those in which the body or its covering is everywhere of the same hue, or nearly so—as in the elephant, the wild buffalo, or the house mouse in which the hairy covering (or hide in the elephant) is of a nearly uniform tone everywhere. So too, the crow, the apteryx, and the nestlings of many birds whose parents show a more highly differentiated style of markings. Such mammals and birds, so far as the development of pattern is concerned, I would consider unspecialized, yet it does not follow that in this respect they are also primitive, though in most cases I venture to think this may be true. The uniformity of plumage is probably a derived condition in such a species as the Cuban blackbird (*Holoquiscalus assimilis*) in which the duller colored females have yet a yellow patch at the bend of the wing, a style of marking widespread among allied forms. The adult males, however, have lost this and are wholly black. Gadow as well as Keeler (1893) conclude that among related species in which there is a tendency to differentiation of the coloring the end result of the stages through which the species may pass is the production of a wholly black bird. In general a wholly black condition is no doubt to be considered as a derived rather than a primitive state among birds whereas a uniformly dull plumage of a brownish or grayish tone is probably in most cases primitive. Among mammals the same is probably also true, for in both the black condition indicates either an excessive production of the black over other associated pigments, or a loss of the power to produce the latter, whereas the neutral gray or brownish coloring is due to a more even mixture of such pigments.

As pointed out by Professor W. E. Castle, the "ticked" pattern of the hairs of mammals is probably primitive, and it is certainly very widespread. It is well illustrated, for example, by the house mouse (*Mus musculus*) or the wild guinea-pig (*Cavia*), in which three separate pigments occur as granules in the individual hairs—yellow, chocolate, and black. These three in their normal mixture produce a neutral gray tint—mouse color—and an examination of this type of coat usually shows that some hairs are wholly black, others dark at base barred with black and yellowish near the tip.

There are two ways in which patterns may be developed from a uniformly tinted covering of hair or feathers: (1) by a local change in the relation of the associated pigments so that in certain areas only one or two sorts are produced instead of three, or only one; (2) by a failure to develop pigment at all in certain places, so that a white or unpigmented area is produced.

It is not rare among mammals to find that one or more of the characteristic sorts of pigments are not produced in certain individuals and probably the factor or factors for these are lost altogether from the somatic and sex cells alike. Such variations may be perpetuated through inbreeding and so no doubt have arisen sundry domestic color varieties of animals and plants. For example, in the course of experiments with color varieties of the house mouse (carried on some years since with Professor W. E. Castle) we found that the chocolate-colored mice which we bred as extracted recessives from black mice, contained only chocolate pigment in their hair, whereas in the black parents both black and chocolate pigments were present, but the black masked a chocolate pigment. Moreover, the chocolate mice always bred true to that color, but if bred back to the black parents, gave black young or both black and chocolate in Mendelian proportions, according to the nature of the matings. The interesting point here is that the chocolate mouse once produced, through the loss of its black-and-gray-pigment-potentiality, can transmit no other pigment character but the chocolate. What causes the occasional production of an individual in which one or more of the characteristic sorts of pigment is absolutely lacking is still unexplained. Nevertheless it is of frequent occurrence not only among domesticated species, in which the natural conditions of life are so greatly modified, but also in species in a state of nature.

A skunk normally marked, but chocolate instead of black, a raccoon likewise of normal pattern but the pigmented areas yellow, are merely examples of the dropping out of the factor for black pigment from the normal combination of the two. Such specimens are of occasional occurrence, and examples are in the museum of the Boston Society of Natural History. Similarly are produced red woodchucks or muskrats, or wholly yellow field mice (*Microtus*). Melanism commonly results through an excess of black pigment which may mask a second pigment. Thus the black hairs of the black variety of fancy mouse commonly contain a considerable amount of chocolate pigment as well, and so of the hairs of the black-appearing skunk. A black mouse thus does not contain the yellow pigment, while the chocolate pigment is largely masked in general view by the black. In other cases it may be that black pigment alone is present.

It is probable that many cases of dichromatism among animals are explicable as similar cases in which one or other of the pigments normally present becomes to a greater or less degree inactive. Thus red forms of certain blackish or dull-colored bats (*e. g.*, the small *Molossus* of Cuba) are apparently the result of the dropping out of the factor for black pigment or its great reduction. The red and gray phases of the screech owl (*Otus asio*) are probably also explicable as a similar phenomenon.

It is only when this inactivity of one or more of the pigment factors occurs locally on the body that a definite color pattern is produced, in which neighboring areas of the body are of contrasting hues. As an example may be cited the variegated guinea-pigs, whose monotone ancestors are still abundant in a wild state in South America. Professor Castle, through his studies of these patterns in guinea-pigs, first suggested to me in 1903 that there were definite areas of the body which, though contiguous, are independent of each other in their pigment-producing capacity. In this suggestion lies the key to the chief investigation of this paper, namely, the defining of these areas, and a study of their behavior in the development of pattern by the second of the two methods previously given—that is, through the failure of pigment to develop, so that white or colorless areas result. This condition of partial albinism is not uncommon among animals which in their normal condition are completely pigmented. In domestic species it is very general and in them tends to be preserved. It also occurs normally in the shape of definite white markings in the patterns of many mammals and birds. Magazines of natural history abound with instances of total or of partial albinism among mammals and birds, either of domesticated or of wild species. Some writers have even recognized the fact that such white markings tend to occur in certain parts of the body, as at the tip of the tail or on the forehead. Darwin speaks of the white forehead spot or star, and the white feet so common among horses, and implies that such markings must be of some significance. His statement on hearsay that white-marked horses are more susceptible to poisoning from noxious herbs is, however, uncorroborated. In 1882, W. H. Brewer gathered a number of statistics as to the presence of white marks in horses and cows, but reached no conclusion. He could find no necessary correlation between the presence or absence of white spots in forehead and feet, though it appeared that white marks might be more frequent on one side of the body than the other. But the tentative conclusion that such animals habitually reclined on the side showing the more white, is begging the question.

As briefly stated in my paper of 1904, the important thing is not that white tends to appear at certain places, but the converse, that pigment production is more intense at certain definite centers on the body and the occurrence of white or pigmentless areas is due to the restriction of pigment formation at the periphery of these centers, so that white occurs at their extremities or as breaks between contiguous color patches.

In mammals and birds these centers are typically five on each side of the body, and a median one on the forehead. They appear to be homologous in both groups, though in different species they show varying degrees of modification in their behavior and development. When a reduction of the pigment areas occurs, the appearance is as it were a shrinking of the particular color patch toward its definite center. The reduction may vary to any degree, from that condition in which the break between two adjacent patches is merely indicated by a white streak to that in which it is reduced to a small spot of pigment, or to zero, when the entire patch drops out, leaving a white area. These patches are wholly independent of each other in the extent to which they may be developed, so that a particular patch may be quite wanting on one side of the body, while its fellow of the opposite side is completely developed. Nevertheless, there is often a marked tendency to bilateral symmetry in such reduction. From a study of partial albinos in which the pigment reduction is considerable, the location of the ultimate centers of these patches becomes possible as well as the determination of their normal extent. I have studied several domesticated species in which white marks are common, with the results briefly detailed below.

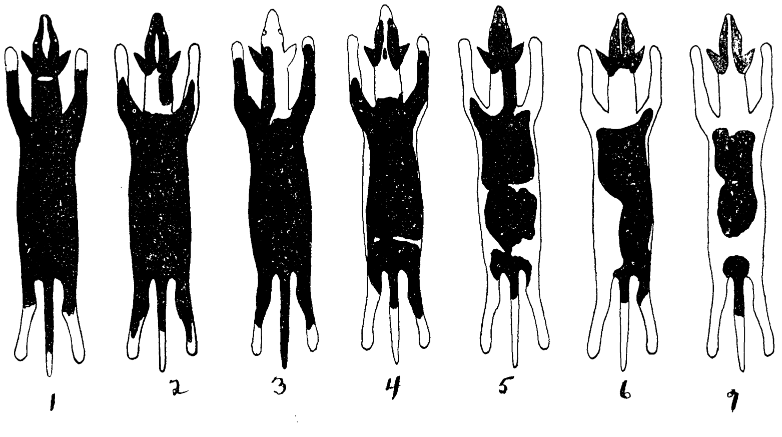
When all the centers are fully developed the animal is completely pigmented; when none is developed, it is a total albino. Between these extremes may be found every conceivable degree of development. In an ideal case in which each center is slightly reduced so as to be circumscribed by white, the animal would have a dark coronal or crown patch and a series of five patches on each side separated by a median dorsal and a median ventral stripe. The anteriormost of the lateral patches center at the base of each ear, and each in its greatest development covers the side of the head from muzzle to behind the ear. These I have called the aural or ear patches; the next posterior are the two neck or nuchal patches each of which pigments its proper side of the neck, and extends from behind the ear to the shoulder and anterior edge of the foreleg. When much reduced the patch, as it were, contracts to a small area on each side of the neck, varying slightly in its location among different species. Posterior to these come the scapular or shoulder patches one on each side of the body. Each pigments the shoulder area and foreleg, except (usually) the front edge of the upper part of that member. This patch shows interesting slight variations in the extent over which it spreads in different species. Centering nearly at the lower part of the back are the pleural or side patches, each of which pigments the area from the shoulder to the lumbar region and anterior part of the hind leg of either side. Last of all, the two sacral or rump patches, each of which on its respective side pigments the buttocks and tail. In most species these two patches are so closely associated that they tend to remain fused dorsomedially, so as to give the appearance, when reduced, of a single median patch at the base of the tail. Their frequent bilaterality, however, indicates the dual origin of such median patches. Each of the lateral patches in its complete development extends from the mid-dorsal to the mid-ventral line or those of opposite sides may overlap slightly. Reduction usually first appears mid-ventrally.

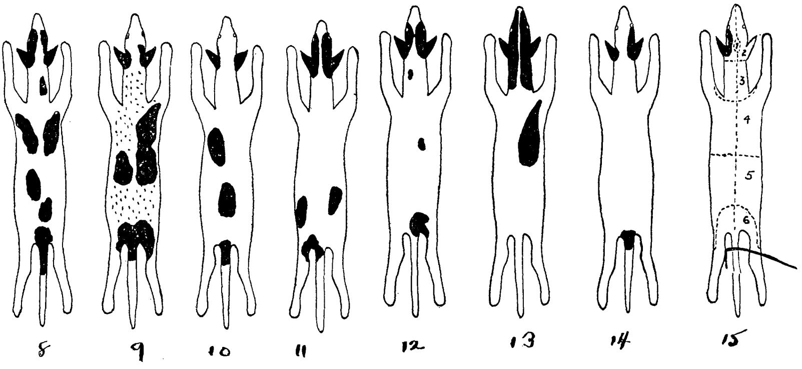
It is probable that the retinas should also be considered as an additional pair of patches, since morphologically the eye is of dermal origin, and there is sometimes seen a tendency to the formation of a small circumorbital patch, which appears to break from the ear patch when this is largely reduced.

Pocock (1907) has pointed out that in black-and-tan dogs the tan appears about the muzzle, along the sides and on the limbs, while the blacker portions are more dorsal. It may be added that in tricolor hounds, in which the several primary patches are reduced, these are often tan color at their several peripheries and black centrally. In both cases, the explanation is simply that pigment formation is less intense the farther away from the primary centers.

The reason of the division of the body surface into these independent areas of pigmentation does not here concern me. It is no doubt the result of physiological causes, and it is rather suggestive that the several patches correspond externally to important nerve centers or groups of nerves. Thus the eye pigment corresponds to the optic nerve, the aural patch to the auditory nerve, so that these two great external sense organs of the head have each their corresponding pigment patch. The neck patch corresponds with the group of cervical nerves, the shoulder patch with the brachial plexus, the side patch with the nerves of the trunk, and the rump patch with the sacral plexus. It may be further suggested that the median crown patch of the head corresponds to the pineal eye, a suggestion that is strengthened by the fact that it is more or less obsolete in mammals, just as the pineal gland is vestigial, whereas in birds, which are more reptilian in structure, the patch is usually well defined. At all events it is a median unpaired structure, as are the pineal and the interparietal bone.

Turning now to a more detailed consideration of these pigment patches in sundry species of animals, we may first examine a series of diagrams (Figs. 1–15) of the





FIGS. 1–7. DIAGRAMS ILLUSTRATING PIGMENTATION IN THE DOMESTIC DOG.
FIGS. 8–15. DIAGRAMS ILLUSTRATING PIGMENTATION IN THE DOMESTIC DOG.

domestic dog, all of which are carefully drawn from photographs or from living animals, and are selected from a great number to show various conditions in the reduction of the pigment patches. In these and the other diagrams the black portions represent pigmented areas, irrespective of the actual colors.

For convenience I have called the white stripes demarking these chief or primary patches, "primary breaks," since they are the first indications of a decrease in pigmentation such that two adjoining patches no longer meet. Secondary or further breaks result in a general disintegration of these primary pigment patches, and are apparently more irregular in nature, though often they follow certain fairly well defined lines. The first of the primary breaks generally occur as white patches on the chest or belly, about in the median line. These are not shown in the dagrams, but in most cases should be understood as present. In Fig. 1 the pigment areas show a beginning in reduction. The two aural patches have become separated and their failure to spread to the normal limit in the median line has resulted in a white nose stripe. A short transverse white marking indicates a separation of the neck patch at its anterior edge from the ear patch. Elsewhere the various patches are contiguous; but the extremities of the limbs and tail are pigmentless, as if pigment had failed to spread to the tips of these members in its reduction. In Fig. 2 the same primary break between the ear patches is present, and in dogs it is one of the first and most frequent to appear. The same shrinkage of pigment from the extremities is also seen. The neck patch of the left-hand side, however, has completely dropped out, and its fellow of the right-hand side is reduced posteriorly so that it fails to reach the shoulder patch. Thus a white collar is formed. It is also interesting to see that at its anterior end a distinct constriction is present where the neck patch joins the ear patch of the right side. Fig. 3 shows a somewhat similar condition but the neck patch of the right side as well as the ear patch is missing, while those of the left side are fully developed. In Fig. 4 both neck patches are missing, so that a white collar is formed. In dogs the neck patch is usually the first to drop out altogether, so that a white-collared dog is of very frequent occurrence. In fox hounds this patch is shown unusually well, either wholly or partly separated from neighboring patches. The separation of the ear patches, wholly or partially, so as to produce a white blaze or line in the middle of the forehead is about as frequent. In Figs. 8 and 12 a single neck spot only (as it happens, in one on the right, in the other on the left side) is still present but so slightly developed as to be only a small island of pigment wholly separate from the neighboring patches.

The crown spot is so often present in dogs as a little oval island, always on the top of the head about in line with the anterior bases of the ears (Fig. 4) that I am convinced it is a primary patch. It is common in bull dogs and bull terriers, and in other breeds is often seen but is so commonly not indicated at all, that it seems probable it is becoming lost, and its area is filled by the ear patches, since these are often separated by a very narrow median line only, which, as in Fig. 13, may continue posteriorly to separate the two neck patches medially as well. In other cases (Figs. 1, 6) the failure of the white nose stripe to extend farther posteriorly may be due to the persistence of this patch.

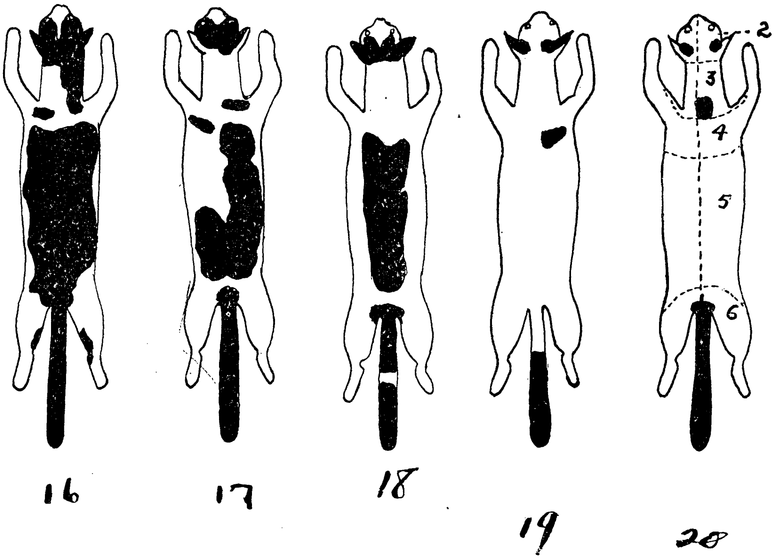
The demarcation of the side from the rump patches is indicated by the imperfect primary break across the lower part of the back in Fig. 4, while in Fig. 5, a similar primary break farther forward indicates the limits of the shoulder and side patches. In each case the break is incomplete transversely, with a narrow isthmus near the median line. In dogs there is a marked tendency for the ultimate centers of the side and rump patches to be close to the median line, so that the corresponding patches of opposite sides are confluent dorsally. This is especially the case with the rump patches, with the result that it is very rare to see the two rump centers separated, but instead, as in Figs. 10 and 14, they appear, when much reduced, as a small median spot at the root of the tail. That they were originally paired, there is no doubt, as there is frequently (as in Fig. 9) a deep median notch indicating the median primary break between the centers, or (as in Figs. 11, 12) one of the lateral centers drops out, leaving its fellow of the opposite side. The continued union of the side patches with the shoulder patches is seen in Fig. 7, while in Fig. 9, though the union is still present between these patches of the right side, on the left side the shoulder patch has failed to develop, and the side patch is so reduced that it does not meet its fellow of the right. In Fig. 8 both shoulder patches are present more or less bilaterally equal, and, as frequently, are produced into narrow tongues on to the upper arm. The two side patches in Fig. 8 are also reduced, so as to be wholly separated from each other and from the neighboring centers. They are further interesting in being placed nearly median one behind the other instead of nearly opposite. In Fig. 11, on the other hand, they are far sundered, but this, in dogs, is a much less usual condition. In Fig. 10 a single median dorsal patch represents the slightly developed side patches, but whether this single patch corresponds to one or other of the two centers, or whether the two are actually fused in the dorsal line, I can not yet say.

The shoulder centers, when slightly reduced, are large in dogs, and cover a considerable saddle-shaped area, as indicated in Fig. 5, from near the center of the back forward including the fore leg and part of the fore shoulder. When further reduction takes place the pigment is drawn away from the extremities and the saddle separates from the neck patch (Figs. 2, 6) and then from the side patch (Figs. 5, 9), and finally the shoulder patches separate from each other (Fig. 8). One or other of the shoulder patches may drop out entirely (Fig. 10) or be reduced to a very small spot (Fig. 12) at what may be considered the ultimate center of the pigment patch, near the upper part of the body, near or just back of the shoulder. The ear patches seem to be the last to disappear, and these, too, may be variously reduced or only one may be present (Fig. 15). The approximate outlines of the patches when fully developed are indicated by dotted lines in Fig. 15, in which 1 is the crown patch, 2 the ear patch, 3 the neck patch, 4 the shoulder patch, 5 the side patch, and 6 the rump patch.

In dogs, there is seldom seen any tendency for these primary patches to divide. What has the appearance of such a tendency is seen, for example, in the coach dog, which is rather evenly flecked with rounded black spots, with often in addition, black ears and more rarely reduced rump patches. Fig. 9 shows such a dog in which both ear patches, one shoulder, both side and both rump patches are sharply indicated, though reduced. In addition there are present on the white body areas between, many small flecks of dark color, evenly distributed, which are clearly not islands separated from the primary patches. Indeed this spotting seems to constitute a wholly different category of pigment formation, in addition to that of the primary patches, which latter I have called "centripetal" pigmentation. As Professor Castle suggests to me, it is probably homologous with the "English" marking or spotted condition of domesticated rabbits, and possibly the dappling of horses is a similar phenomenon. When these spots and the primary color patches are of the same hue, it is not possible to distinguish the two in visual appearance, unless the latter are reduced areally, when, as is sometimes the case in the coach dog, one or more of the primary patches is seen with the spots, as it were, proliferating from its edge. This second element no doubt enters as a factor in the color pattern when the small spots are of a different color from that of the general body surface, as in case of the cheetah (*Cynælurus*) or the leopard and jaguar.

I am inclined to think that the excessive breaking up of the primary patches, to be considered under the cow, is not a wholly similar phenomenon.

Five diagrams illustrating the domestic cat are shown in Figs. 16 to 20, and are interesting to contrast with those of the dog, also a carnivorous mammal. The demarcation of the primary patches is usually less sharp than in dogs, but is in general similar. The most common appearance is where the primary breaks occur in the mid-line below, giving a white throat, chest or belly; or the separation of the aural centers produces a white streak on the nose or extends it up between the ears. The ear patches in Figs. 17, 19, 20, show successive reduction, so that at first the hinder margin of the ears, as in dogs, becomes white, then with further decrease in pigment production, the inner bases only are colored. The neck patch has its ultimate center farther back than in dogs so that when much reduced, it is present as a pigmented spot at the very base of the neck or even at the front of the shoulder (Figs. 16, 17). In Fig. 16 the neck patch of the right-hand side is only slightly reduced and is in contact anteriorly with the ear patch, while poste-



FIGS. 16–20. DIAGRAMS ILLUSTRATING PIGMENTATION IN THE DOMESTIC CAT.

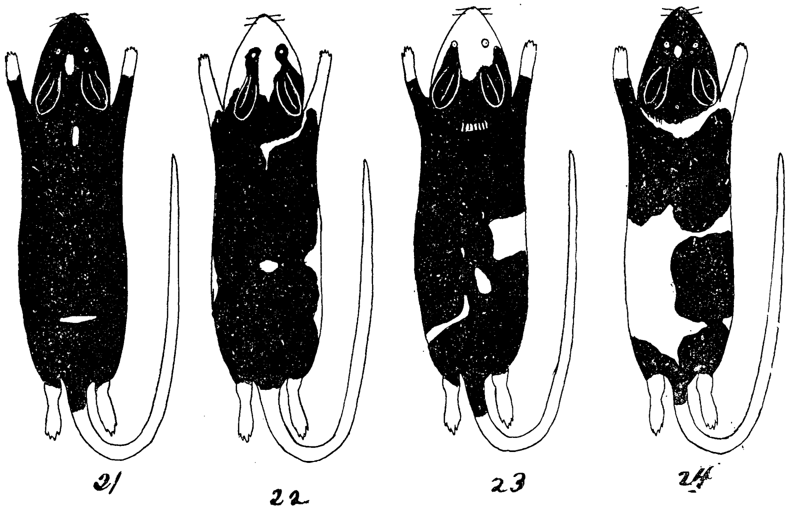
riorly it does not meet the shoulder patch. The left-hand neck patch, however, is quite separate from the neighboring patches and is reduced to a small area at the junction of the neck with the shoulder. It is absent in Fig. 17 from the left side and is represented on the right side by a similar small center, placed far back. In Fig. 20 the neck patch or patches show a reduction to a single small square median patch at the base of the neck, but whether this represents a median fusion of the two lateral centers, or whether one only has persisted and has shifted to the midline, I do not attempt to say, though the former hypothesis seems on the whole more probable.

The shoulder patch in house cats is relatively small, and, as indicated by the indentations in Figs. 17, 18, is of the fore side of the upper arm, but the shoulder patch when fully developed seems to cover the rest of the leg and a small scapular area. It is shown much reduced in Fig. 19, on the right-hand side, and is altogether wanting in Fig 20. The conjoined shoulder and side patches in Fig. 18 are shown reduced laterally, so as to form a broad median stripe which I take to mean that the ultimate centers are closely approximated dorsally. The neck patch is wholly absent, but both ear patches are present and joined medially. The sacral patches, as commonly, seem fused or at least very close together. There is a small break midway on the tail, which separates off a pigmented tip, a phenomenon which I shall refer to under ''centrifugal pigmentation.'' The side patch is long comparatively, and extends forward to cover the deficiencies of the shoulder patch, as in Fig. 17. Here the left side patch has been reduced at its anterior end, and its separateness from the patch of the right side is indicated by the median indentations. It is often wanting in domesticated cats.

The sacral patches, pigmenting the buttocks and tail, seem to be fused or closely approximated at the root of the tail, as in dogs. I have seen no instance of the crown patch being shown in the cat, though such may occur.

The approximate boundaries of the five bilateral patches are indicated in Fig. 20 by dotted lines; 2 is the ear patch, 3 the neck patch, 4 the shoulder patch, 5 the side patch, and 6 the rump patch.

Among domesticated rodents the pigment patches have been studied in rats, house mice, and guinea-pigs. In all, the same patches appear except that in rats and mice the median crown patch appears to be lost, though in the guinea-pig it is often present. Diagrams of parti-colored mice are shown in Figs. 21–24, and sufficiently indicate the primary pigment areas. The white spot on the forehead of Fig. 21 indicates a primary break between the two ear patches, and varies widely in different individuals, from a few white hairs only to a large blaze The inheritance of such a blaze has been studied by Little (1914). The white mark at the base of the neck in Fig. 21 indicates the beginning of separation of the neck from the shoulder patches and perhaps of the two neck patches from each other, because of its longitudinal extension. The white band across the neck in Fig. 23, however, indicates probably only the beginning of a separation of the neck from the shoulder patches, which in Fig. 24 has



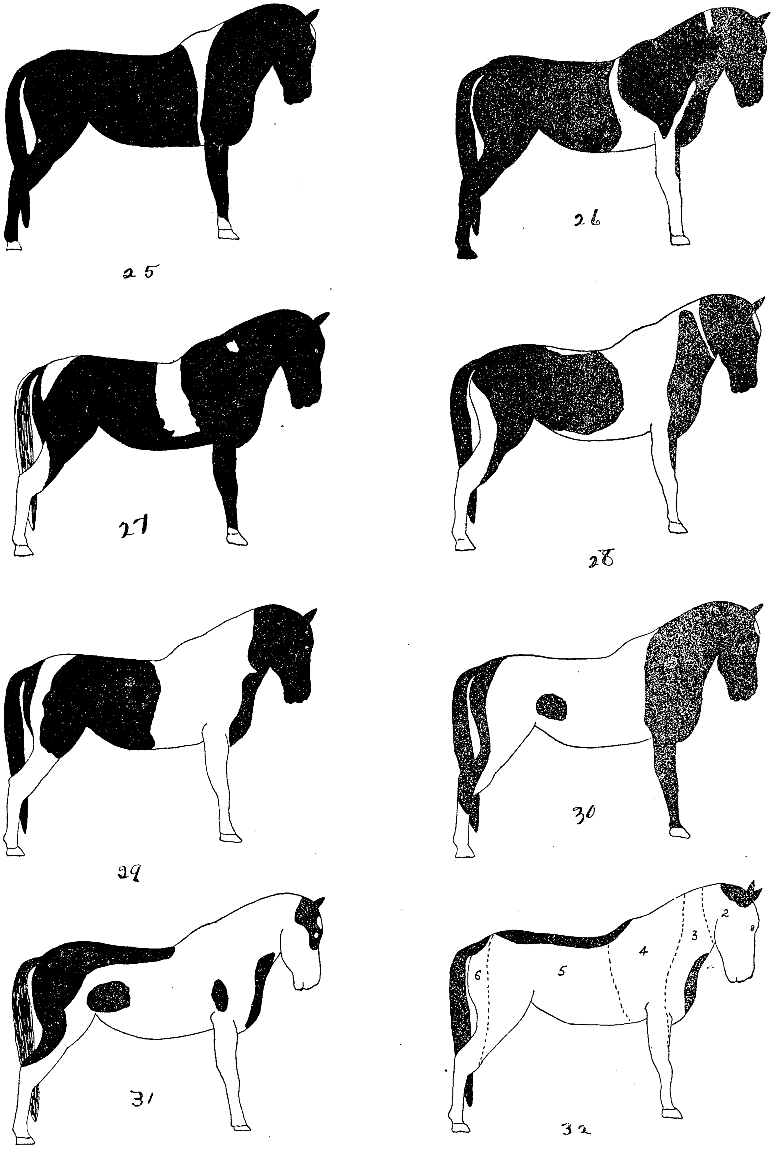
FIGS. 21–24. DIAGRAMS ILLUSTRATING PIGMENTATION IN DOMESTIC VARIETIES OF THE HOUSE MOUSE.

wholly sundered these two areas, so that a white-collared mouse results. The condition shown in Fig. 22 is similar, except that the separation has taken place on the right side only, between the neck and the shoulder patches of but one half of the body. A break between the two neck patches of opposite sides is further indicated in this figure by the deep median reentrant back of the ears.

In all four diagrams the areal restriction of the shoulder patches is shown, but in varying degrees. In Fig. 21, the pigment has not spread to the feet, leaving these white, and so in the other figures, but to a greater degree. A median linear break between the shoulders indicates the restriction of the patches of opposite sides at this point, which in Fig. 22 is more clearly perceptible. The posterior limits of the shoulder patch are further shown in this diagram, by the beginnings of a break between the shoulder and the side patches. In Fig. 24 this break is no longer interrupted, but clearly separates the two areas. Further, the side patch has dropped out on the left. In Fig. 23 an imperfect separation of patches on the posterior part of the body has taken place. On the right-hand side the shoulder patch, which in mice is of considerable extent, has broadly separated from the side patch, while on the left-hand side a long transverse break has taken place between the side and the rump patches, with two island-like white spots between, the anterior of which probably marks the transverse line of stress between shoulder and side patches, the posterior the median line of breaking between the two side patches. A slight indentation in the pigmented area far back on the right side of Fig. 22 points to the beginning of restriction between side patch and rump patch. The separation of these patches by a transverse mid-dorsal break is shown in Fig. 21, and their complete separation on the left side appears in Fig. 23 (the transverse white mark), while in Fig. 24, owing to the failure of the left-hand pleural patch to develop, the two rump patches, both partially separate from each other, are wholly disconnected from the former except by a narrow isthmus on the right side. The long tail is usually without pigment, or mainly so where areal restriction is present, and it is seldom that pigment extends far on to the base of this member when the restrictive tendency appears. In the domesticated varieties of rats, the same patches may be distinguished. There is, however, an interesting variety known as the "hooded" rat, in which the ear and neck patches appear to be normal, but a narrow median dorsal area is pigmented for a varying length, sometimes quite to the root of the tail. A separate factor seems here to be involved, producing what may be called a "centrifugal" type of pigmentation, which in many forms of mammals causes a black spine stripe (*Sorex wardi, Tupaia tana,* certain forms of Apodemus, *Equus caballus*), and others.

Among guinea-pigs the typical primary patches are beautifully shown and may be seen in sundry figures published in papers by Professor Castle on heredity in this animal. The guinea-pig is one of the few mammals yet known in which the median crown patch is visibly present, a character which I take to be primitive.

In guinea-pigs the breaking up of the ticked color pattern has progressed under long domestication to an extraordinary degree, so that not only are black, tawny or grizzled animals produced in various shades, but even in the same individual, *the different primary pigment areas may be of different colors.* This fact is of much significance, for it indicates not only the mutual independence of the contiguous color areas, but further points to the manner in which a variegated color pattern may have been acquired. Among mammals the color pattern is in general, not greatly developed in comparison with birds, yet in many cases where some modification has taken place, it is evident that this differentiation is confined to the limits of one or two of the primary pigment patches. Thus in the South American Tayra (*T. barbara*), the head and neck are a grizzled gray, and the breaks occurring in pied individuals show that the grizzled condition



Figs. 25–32. Diagrams Illustrating Pigmentation in Horses.

is confined to the aural and nuchal patches only, for elsewhere the animal is black. In this case, too, the black condition is probably derived, for youngish animals are uniformly grizzled, and sometimes, apparently, this is the adult condition as well.

Among domesticated ungulates the same primary patches are to be distinguished in cases where partial albinism renders their bounds apparent, with the exception that in horses, cows and deer I have seen no clear indication of the median crown patch which in mammals is probably obsolescent.

In both horses and cows the patches show interesting and peculiar modifications. A series of diagrams (Figs. 25 to 32) show these patches in "calico" horses, though not so fully as could be wished. The first indications of areal restriction of pigment in horses appear in the shape of a white "star" or round spot in the center of the forehead. This is often accompanied by white at the base of the hoofs, or sometimes the entire foot is white producing the so-called "white stockings." But there is no necessary correlation between these white areas, such as Brewer (1882) tried to show. The white on the forehead may vary from a few white hairs to a broad blaze covering the entire front of the head between the eyes to the muzzle. Sometimes the restriction of pigment is such as to produce in addition to the white star on the forehead, a white spot over each eye, and sometimes these three spots are joined by a narrow unpigmented area. This indicates that pigment production is weak at a spot directly over the eye in comparison with neighboring parts, and this no doubt accounts for the fact that in black-and-tan or other dogs these are the pale spots over the eyes where black pigment is not produced. A white spot over the eye is also characteristic of many rodents.

Next after the restriction of the ear patches and the drawing away of pigment from the feet, the most common white marking seems to be a primary break, as in Fig. 25, from the shoulder back of the foreleg, which delimits the posterior border of the shoulder patch. In the horse the shoulder patch is large, and differs from that of any mammal I have yet studied, in its great extent forward along the dorsal side of the neck nearly to the head. In Fig. 26 a small break at the back of the neck indicates the beginning of separation between the ear and the neck patches dorsally, and a long tongue of white running upward from the forearm indicates the anterior limit of the shoulder patch. This limit is marked still nearer the dorsal line in Fig. 27 by a white spot on the side of the neck near its base. In Fig. 28 the shoulder patch has entirely dropped out and the white space outlines very nearly its extent. The ultimate center is perhaps shown by the small shoulder spot in Fig. 31.

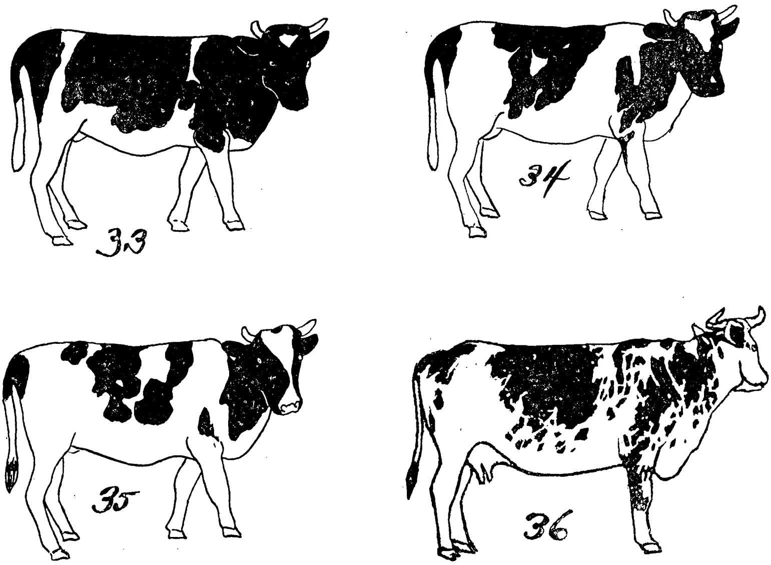
The area covered by the ear patches extends well on to the upper part of the neck, and in Fig. 29 is shown at its greatest spread, or, as in Fig. 28, cut off by a narrow white collar from the neck patch. The neck patch is remarkable from the fact that in its areal reduction it becomes restricted first dorsally, and the ultimate center of each side is nearly ventral on the throat, so that, as generally seen, the two centers form a single median patch on the front or ventral part of the throat. In Fig. 26 the neck patch is seen to pigment the anterior side of the forearm and is partly separated from the shoulder patch by a long tongue of white. It seems to extend up diagonally to reach the mid-line of the neck for a short distance only, as indicated in Fig. 28, where its bounds are only slightly contracted. In Fig. 29 it is so far lessened as to be absent from the forearm, though still in contact at the throat with the ear patch where, however, a deep indentation locates the dividing line between the two patches. In Fig. 31 a median ventral division of the conjoined neck patches is seen indicated at the upper part of the area, which in this case no longer reaches the ear patches. Still further reduction of both ear patches and neck patches is seen in Fig. 32, but, as commonly, the neck patches seem fused in the midventral line. This shifting of the neck centers ventrally is a rather remarkable phenomenon which may have some relation to the manner in which the head is held erect. For this reason it might be expected also in antelopes, and is perhaps evidenced in such a species as the oryx, in which there is a black median line on the throat as though strongest pigment production centered there rather than on the gray sides of the neck. The median reduction of the shoulder patches in horses is sometimes indicated by a white mane.

The rump patches in the horse appear to be much as in other mammals, restricted to the tail and posterior part of the buttocks and the entire foot. In Fig. 30 the patch is shown at nearly its full development, except that it has failed to extend to the entire hind foot. In Fig. 27 it has drawn away still farther but remains in contact with the side patch at one place. In Fig. 29 it is further restricted to the tail and posterior border of the haunches, while in Fig. 32 it covers only the root of the tail and that member.

The side patch is the largest of all and extends from the shoulder to the fore part of the haunches and on to the fore part of the hind leg nearly to the foot, as seen in Figs. 27 and 28, where it is still in contact with the rump patch, or in Fig. 29 where it has become separated. In its further reduction this patch may appear as a small spot back of the ribs or, as often, a curious division takes place, separating the patch into a dorsal area and a lateral one. Occasionally this secondary break appears in a horse which has most of its patches otherwise well developed. In Fig. 31, the pigmented area of the tail, buttocks and lumbar region consists of the conjoined rump patch and a dorsal portion of the side patch, while the *ventral* part of the side patch is present as the oval spot at the groin. In Fig. 30 the latter spot only persists, but in Fig. 32 the dorsal portion of the side patch alone is present as a stripe along the entire back, except where it breaks away posteriorly from the small rump patch.

This peculiarity of the side patch in horses is somewhat paralleled in cows by a tendency to secondary breaking up, though in a different way, as detailed below. It is significant in this connection that in horses and donkeys there is usually a black stripe along the spine from shoulder to tail which may indicate that "centrifugal pigmentation" is also present (see beyond). The dotted lines in Fig. 32 indicate the approximate boundaries of the several primary patches. The crown patch seems to be wanting in horses; 2 is the ear patch, 3 the neck patch, 4, 5 and 6 the shoulder, side, and rump patches, respectively.

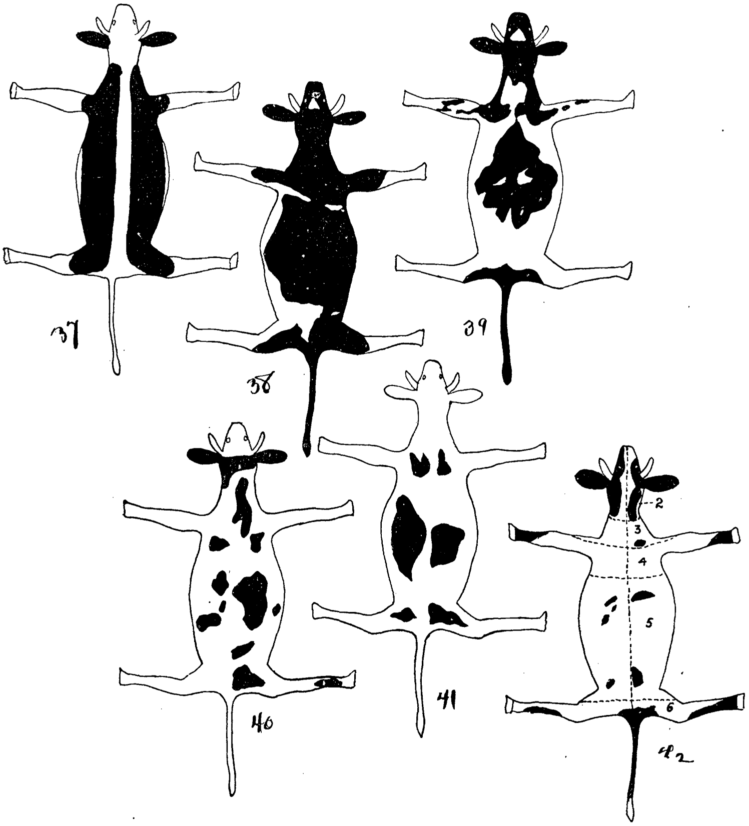
Of domestic ruminants I have studied the pigmentation in the cow and show in Figs. 33 to 42 a few of the many variations in partial pigmentation. These are all drawn from photographs or from the animals themselves, and are of cows in which, so far as I know, there has been no attempt at breeding for pattern. Two types of spotting may be distinguished in cows: first, that in which the pigmented areas are sharply outlined and solid or at least



FIGS. 33–36. DIAGRAMS ILLUSTRATING PIGMENTATION IN DOMESTIC COWS, SIDE VIEW.

practically so; second, that in which there is a greater or less tendency for the primary patches to be much broken up into small islands (as in Fig. 36) by secondary breaks, though the main areas are still distinguishable. I take this second or fragmental type to be a different phenomenon from the diffuse or dappled condition seen in the coach dog or the dappled-gray horse.

In the cow, the ear patches as usual pigment each its proper side of the head to a short distance behind the ears. The point of separation between ear patches and neck patches is indicated by a small break back of the skull in Fig. 38, while the posterior extent is shown by the two ear patches in Fig. 42. These patches usually



Figs. 37–42. Diagrams Illustrating Pigmentation in Domestic Cows, as Seen Spread Out and from Above.

draw apart first across the forehead making here a triangular white mark, and on the muzzle, as in Fig. 34. Further restriction broadens these white marks and joins them by a narrow isthmus as in Fig. 35. In Fig. 40, the two patches are still conjoined across the vertex, but are much reduced, that of the right side more than that of the left. In Fig. 42 they have failed to join medially, though fairly well developed longitudinally. Still greater reduction, as in Fig. 37, confines them to the ears, the bases of which appear to be the ultimate centers.

The neck patch in the cow is more extended posteriorly than in the horse, and its center is strictly lateral rather than nearly ventral. It is shown in Fig. 34 somewhat contracted from the mid-line of the throat, but extends squarely back against the foreshoulder at the base of the neck, and is fused near its ventral corner with the small shoulder patch, itself much reduced. As in other mammals it appears to extend in its complete development, to the front edge of the upper foreleg. The animal in Fig. 41 shows a bilaterality in its pigmentation that is rather unusual. What appear to be the reduced neck patches are seen far back at the border of the foreshoulder. In Fig. 40 the left-hand neck patch has dropped out, but that of the right side is still present, though small, and in Fig. 42 it is reduced to a small spot only.

The shoulder patch in cows is remarkably narrow, and compressed between the neck patch and the body patch, whence it extends as usual on to the foreleg. In Fig. 33 a primary break back of the foreshoulder marks the nearly vertical posterior outline of the shoulder patch. In Fig. 34 the separation of this area from the neck patch is all but complete and the patch itself somewhat reduced. Its narrow vertical outline is thus indicated, as well as in Fig. 39, in which there is a narrow tongue-like extension down on to the center of the foreleg.

In its further reduction it appears as a small center at the base of the scapula, as in Fig. 35, or in Fig. 40, in which both shoulder patches are present, though small. In Figs. 41 and 42 the shoulder areas are wanting. A very common mark in cows is a white belt just back of the foreleg. This is due to the development of a primary break between shoulder patches and side patches, a condition which is nearly realized in Figs. 33 and 38. It is probable that this marking has been more or less fixed through selection in breeding, and this has been the more readily accomplished, since this break occurs in a place which is one of the first in cows to cease pigment production.

The side patch is large and covers the entire lateral region of the body from the scapula to the hips, and on to the front edge of the hind limb. When only slightly reduced, it appears as a blanket-shaped area across the back as in Fig. 38, where it has not wholly broken away from the shoulder and rump patches, or as in Fig. 33, where it has become nearly separated. In its further reduction this dorsal blanket shows a peculiar manner of breaking up into more or less transverse stripes directed slightly backward. The beginnings of these secondary breaks appear in Fig. 39 in which are seen on each side posteriorly two deep indentations at the edge of the patch, whose points if extended would meet the white pigmentless islands already present within the patch. In Fig. 34 a similar series of indentations points to the trisection of the side patch which is realized in Fig. 35. Here is a characteristic which if developed might eventually result in the actual production of white stripes on the body, such as are found, for example, in certain antelopes as the bongo and the kudu. The tendency of the side patch to divide into three, as in these diagrams, is rather marked in cows, and even with further reduction the three centers persist fairly well. The first of these secondary centers is just back of the shoulder patch, the second about over the last ribs, and the third over the lumbar region. In Fig. 40 the first two are present on the left side, with a small spot between, which has become separated from one or the other of them, while the third or lumbar spot has dropped out. On the right side, the first and second divisions are still fused dorsally, but the lumbar division is distinct. The same three divisions are seen in Fig. 35, better developed, whereas in Fig. 42, the two lumbars are present, one on each side, and considerably in advance of them, what seem to be the remnants of the first division of the side area, the left one of which has further broken up.

The rump patches show no especial peculiarities, but cover the posterior part of the buttocks and hind legs, and the entire feet and tail. Though frequently the two patches of opposite sides are conjoined medially, they are often, under considerable reduction, well separated. The beginning of such a separation appears in Fig. 38, where there is a deep median tongue of white anteriorly, marking the line of union. In Fig. 41 the reduction has progressed still farther so that the two patches are quite sundered medially and do not extend to the tail. In Fig. 40 the patch of the left side has become inactive, and that of the right side is small.

A curious condition not infrequently seen is shown in Fig. 37, in which all the patches are present, but those of the right side are separated from those of the left by a median dorsal white line, showing the distinct bilaterality of these pigment areas. In the figure, the ear patches are so restricted as not to reach the neck patches of their respective sides, the shoulder patches do not extend far on the forelegs, the side patches are reduced ventrally, and the rump patches, though in contact with the side patches, do not pigment the tail or extremities of the legs. A further reduction of pigment areas results in Fig. 41, in which the paired centers of neck, side and rump patches still appear.

The diffuse condition of pigmentation is illustrated in Fig. 36, which is a photograph, inked in. The ear patch is seen much reduced, but pigmenting the ear. The neck patch is of most irregular shape, with several subsidiary spots separated from its lower border. A clear line separates the neck patch from the shoulder patch, which is also of most irregular boundary. The side patch, at its fore part, is broken into a series of small islands which tend to arrange themselves in lines following the direction of the ribs. The main part of the patch shows a decided tendency to break into the usual three or perhaps four portions. It is common for cows to have patches with very irregular boundaries and tongues of pigment, which may break off into isolated spots in a most bewildering fashion, but even in such cases it is possible to distinguish the main patches of which these form part.

White patches occur in other domesticated ungulates as the pig, the llama, the alpaca, the camel, the yak, the reindeer, and the goat. In the water-buffalo, occasional animals seen in Egypt show a beginning of pigment reduction through the presence of white in the forehead or on the tail. I have had no opportunity to study the markings of these species.

(*To be concluded*)